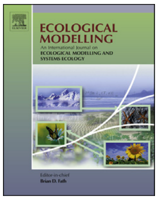
Ecological Modelling 264 (2013) 37–47

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Modeled phytoplankton diversity and productivity in the California Current System

N.L. Goebel[a,*], C.A. Edwards[a], J.P. Zehr[a], M.J. Follows[b], S.G. Morgan[c]

[a] *Ocean Sciences Department, University of California, Santa Cruz, CA 95064, USA*
[b] *Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA*
[c] *Department of Environmental Science and Policy, Bodega Marine Laboratory, Bodega Bay, CA 94923, USA*

ARTICLE INFO

Article history:
Available online 11 December 2012

Keywords:
Diversity
Shannon index
Species richness
Productivity
Phytoplankton
Model
California Current System

ABSTRACT

We explore the phytoplankton community structure and the relationship between phytoplankton diversity and productivity produced by a self-emergent ecosystem model that represents a large number of phytoplankton type and is coupled to a circulation model of the California Current System. Biomass of each modeled phytoplankton type, when averaged over the uppermost model level and for 5-years, spans 7 orders of magnitude; 13 phytoplankton types contribute to the top 99.9% of community biomass, defining modeled species richness. Instantaneously, modeled species richness ranges between 1 and 17 while the Shannon index reaches values of 2.3. Diversity versus primary productivity shows large scatter with low species richness at both high and low productivity levels and a wide range of values including the maximum at intermediate productivities. Highest productivity and low diversity is found in the nearshore upwelling region dominated by fast growing diatoms; lowest productivity and low diversity occurs in deep, light-limited regions; and intermediate productivity and high diversity characterize offshore, oligotrophic surface waters. Locally averaged diversity and productivity covary in time with the sign of correlation dependent on geographic region as representing portions of the diversity-productivity scatter.

1. Introduction

Aquatic ecosystems are characterized by remarkable phytoplankton diversity. One estimate places the number of phytoplankton species in the world ocean at approximately 4000 (Sournia et al., 1991), while counts of freshwater species exceed this by almost a factor of four (Bourrelly, 1985). In limited geographic regions, these numbers are reduced but still high. Cloern and Dufford (2005) observed approximately 500 distinct phytoplankton taxa within the San Francisco Bay estuary and Venrick (2009) documented nearly 300 phytoplankton taxa in the California Current eastern boundary upwelling system.

The general importance of biodiversity in ecology is widely discussed. Phytoplankton diversity in the ocean may influence the functioning of marine ecosystems through, for example, overall productivity, nutrient cycling, and carbon export. Yet most marine biogeochemical or ecosystem models are designed with limited potential for studying phytoplankton biodiversity. Early models included a single phytoplankter and one zooplankter, functionally representing simple predator-prey interactions (e.g., Franks et al., 1986; Fasham et al., 1990). Over the last 15 years, research groups have increased model complexity by including, among other changes, two (Kishi et al., 2007) and three (Moore et al., 2002) autotrophs. Importantly, ocean ecosystem models are now regularly coupled to spatially-explicit ocean circulation models, enabling spatially variable ecosystem response and the potential for niche differentiation among represented species. However, simple and complex ocean ecosystem models to date generally have ignored questions of biodiversity, focusing instead on many other important issues including understanding model dynamics (e.g., Edwards et al., 2000, Spitz et al., 2003), ecosystem response to circulation features (Edwards et al., 2000; Fiechter et al., 2009; He 2011), biogeochemical distributions (Moore et al., 2002) and biogeochemical fluxes (Fennel and Wilkin, 2009; Previdi et al., 2009).

Recently, Follows et al. (2007) developed an ecosystem model that greatly increased the number of competing phytoplankton compartments (to 78) to test phytoplankton community self-organization in a modeled global ocean. Although not all phytoplankton types were suitably adapted to compete effectively for resources, considerably more types were sustained at non-negligible concentrations than possible in more traditional models. Directly calculated diversity indices of temporally and zonally

---

[*] Corresponding author. Tel.: +1 831 459 5152; fax: +1 831 459 4882.
E-mail addresses: ngoebel@ucsc.edu (N.L. Goebel), cae@pmc.ucsc.edu (C.A. Edwards), jpzehr@gmail.com (J.P. Zehr), mick@ocean.mit.edu (M.J. Follows), sgmorgan@ucdavis.edu (S.G. Morgan).

0304-3800/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecolmodel.2012.11.008

averaged modeled phytoplankton revealed largest values in the tropics that decreased with latitude (Barton et al., 2010).

We have coupled this self-organizing ecosystem model to a physical circulation model of the California Current System. Goebel et al. (2010) describe the performance of this model in terms of spatial structure in total chlorophyll concentration, and biogeography and temporal progression of underlying functional groups. However, that work does not examine overall biodiversity or its structure. In this article, we examine output of the self-organizing ecosystem model output in the context of the extensive phytoplankton observations within the CCS. While the overall modeled diversity cannot compare to nature with a limit of 78 phytoplankton types (Goebel et al., 2010), it exceeds the diversity represented in most traditional marine ecosystem models.

In this paper, we examine how modeled diversity relates to productivity using an ecosystem model approach, and then compare modeled trends to those observed in nature. Multiple patterns have been documented and are shown schematically in Fig. 1. Such patterns include monotonic increases or decreases in diversity with productivity and maximum diversity at intermediate productivity that forms a unimodal or hump-shaped curve, often enveloping scattered data, or no relationship at all. The scarcity of observed concave-up (U-shape or inverse hump-shape) trends (e.g., Adler et al., 2011) precludes their inclusion in Fig. 1. Examples of these varied relationships can be found in meta-analyses of mostly terrestrial systems (Waide et al., 1999; Mittelbach et al., 2001) and aquatic benthic communities (Witman et al., 2008). Studies of pelagic aquatic environments have also documented unimodal-like structure, though usually with considerable scatter similar to that conceptualized in Fig. 1d (Agard et al., 1996; Li, 2002; Grover and Chrzanowski, 2004; Irigoien et al., 2004; Duarte et al., 2006; Spatharis et al., 2008). Cermeno et al. (2008) find no statistical relationship in their analysis of coastal, shelf, and open ocean environments. Recently Adler et al. (2011) argue, based on their meta-analysis of terrestrial plants that no simple relationship exists but that many factors contribute to variation in diversity. In this article, we test whether our model results conform to any of these trends in the diversity-productivity relationship using two diversity indices. Subsequently, we use the model to identify geographic regions and associated growth conditions that contribute to the differing portions of the diversity-productivity scatter. Agreement between modeled and observed macroecological patterns improves confidence in using this modelling approach to simulate nature and promotes future testing to determine the importance of representing such diversity in ecosystem models.

2. Methods

2.1. Self-assembling ecosystem model of the phytoplankton community

We investigate simulated phytoplankton diversity and how it relates to productivity using a 3-dimensional ecosystem model for the California Current System. Details of this ecosystem model have been documented previously (Goebel et al., 2010), and we provide only a brief description here.

The ecosystem model has structure similar to many NPZ-type marine ecosystem and biogeochemical models in the literature. At each model grid point, changes in concentrations of inorganic nutrients, phytoplankton, zooplankton, and dissolved and particulate organic matter are budgeted. What distinguishes this model from others is the relatively large number of phytoplankters represented. Here, we resolve 78 phytoplankton analogs. Each analog is randomly assigned parameters that determine physiological responses to light, nutrient and temperature. Parameter values are drawn from distributions constrained by observations and measurements reported throughout the literature. Our maximum growth rates and prescribed distributions of half-saturation levels avoid the initialization of a phytoplankter analog that would outcompete all others. We divide phytoplankton into functional groups based on nutrient utilization, and each functional group is further separated into a multitude of phytoplankton types, distinguished by unique combinations of temperature, light and nutrient responses. Large phytoplankton groups include diatoms, which require silica, and large non-diatoms (LND), which do not. Small phytoplankton groups include *Prochlorococcus*-like phytoplankton (PLP), which do not use nitrate, and small non-*Prochlorococcus* (SNP), which can utilize all three forms of inorganic nitrogen. Within each phytoplankton group, approximately 20 phytoplankton types are initialized. All parameters for phytoplankton losses, and heterotrophic and remineralization processes (e.g., mortality, organic matter export, phytoplankton sinking, grazing of phytoplankton, particulate sinking, nitrification) are fixed rather than randomly prescribed. Size-based differences in sinking and reduced grazer preference for diatoms exist in the model. Phosphorus, nitrogen, and silica budgets are explicit, though phytoplankton concentrations follow Redfield ratios. Biomass and productivity reported in units of carbon are converted with a molar carbon:phosphorus ratio of 106. Carbon is converted to chlorophyll for SNP, PLP, LND, and diatoms as in Goebel et al. (2010). We note that model output used in this study is quantitatively different from than that presented in Goebel et al. (2010) (using, for example, a different random number seed to generate the exact phytoplankton community), but overall results (e.g., of functional group distributions) are qualitatively similar to the previous study.

The ecosystem model is embedded within a physical circulation model that is responsible for advection and diffusion of ecosystem component concentrations. We use the Regional Ocean Modeling System (ROMS; Shchepetkin and McWilliams, 2005), and our CCS domain extends at 1/10 degree resolution from Baja, California to the Canadian border, and to 134 W longitude. A total of 42 terrain-following levels span the water column vertically. The physical circulation is forced by atmospheric fields provided by the Coupled Ocean Atmospheric Mesoscale Prediction System (COAMPS; Hodur, 1997), a high resolution regional atmospheric model, and lateral boundary conditions are obtained from a global ocean state estimate (ECCO, Estimating the Circulation and Climate of the Ocean; Wunsch et al., 2009). More extensive details of the physical circulation model and related applications are published (Broquet et al., 2009; Veneziani et al., 2009a; Veneziani et al., 2009b; Broquet et al., 2010). Model integration extends from January 1, 1999 through December 31, 2004, with the first year treated as spin-up and not included in the analysis.

2.2. Diversity calculations and analyses of biomass and productivity

We assess phytoplankton diversity with two measures: the Shannon index (SI) and a measure of richness. The ecologically-relevant, frequency-based SI is widely used in phytoplankton ecology to portray both species richness and evenness by the uncertainty of sampling such a community at random (Legendre and Legendre, 1998). SI (dimensionless) is calculated as $H = -\sum_{j}^{n} p_j \ln p_j$, where p_j is the proportion of species j to the total biomass. A less descriptive, though perhaps more intuitive, measure of diversity also calculated is simply the number of phytoplankton types that contribute to the top 99.9% of total biomass. We consider this term as synonymous with species richness (SR) when comparing model results to observations. We calculate both SI and SR similarly, within each model grid cell volume daily for